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## THE MENDELIAN INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL<sup>1</sup>

DR. RAYMOND PEARL

MAINE AGRICULTURAL EXPERIMENT STATION

THE investigation here reported was concerned with the detailed analysis and interpretation of a rather extensive series of data regarding the inheritance of fecundity in the domestic fowl. The basic data are derived from trap-nest records extending over a period of years. They include records from (*a*) pure Barred Plymouth Rocks; (*b*) Cornish Indian Games; (*c*) the  $F_1$  individuals obtained by reciprocally crossing these two breeds; and (*d*) the  $F_2$  individuals obtained by mating the  $F_1$ 's *inter se* and back upon the parent forms in all possible combinations. The fully-pedigreed material made use of in the present connection includes something over a thousand adult females, each of which was trap-nested for at least one year, and many for a longer period. This material covers four generations. The birds of the fifth generation have just completed their winter records at the time of writing. Besides this fully pedigreed material, the collection and study of which has occupied

<sup>1</sup> At the request of the editor of the AMERICAN NATURALIST the following summarized account of the principal results of an investigation carried out by the writer has been prepared. A detailed account has been published in the *Journal of Experimental Zoology*, Vol. 13, No. 2, pp. 153-268, August, 1912.

five years, there was available as a foundation, without which the results here discussed could not have been reached, nine years of continuous trap-nest records for Barred Plymouth Rocks, involving thousands of birds, which had been subjected during this long period to mass selection for increased egg production.

Altogether it may fairly be said that the material on which this work is based is (*a*) large in amount, (*b*) extensive in character, and (*c*) in quality as accurate as it is humanly possible to get records of the egg production of fowls.<sup>2</sup> On these accounts the facts presented seem worthy of careful consideration, and to have a permanent value quite apart from any interpretation which may be put upon them.

The essential facts brought out in this study of fecundity appear to be the following:

1. The record of fecundity of a hen, taken by and of itself alone, gives no definite, reliable indication from which the probable egg production of her daughters may be predicted. Furthermore mass selection on the basis of the fecundity records of females alone, even though long continued and stringent in character, failed completely to produce any steady change in type in the direction of selection.

2. Fecundity must, however, be inherited since (*a*) there are widely distinct and permanent (under ordinary breeding) differences in respect of degree of fecundity between different standard breeds of fowls commonly kept by poultrymen, and (*b*) a study of pedigree records of poultry at once discovers pedigree lines (in some measure inbred of course) in each of which a definite, particular degree of fecundity constantly reappears generation after generation, the "line" thus "breeding true" in this particular. With all birds (in which such a phenomenon as that noted under *b* occurs) kept under the same general environmental conditions such a result

<sup>2</sup> Pearl, R., "On the Accuracy of Trap-nest Records," *Me. Agr. Expt. Sta. Ann. Rept. for 1911*, pp. 186-193.

can only mean that the character is in some manner inherited.

The facts set forth in paragraphs 1 and 2 have been presented, and, I believe, fully substantiated by extensive evidence, in previous papers from this laboratory. It is now further shown that:

3. The basis for observed variations in fecundity is not anatomical. The number of visible oocytes on the ovary bears no definite or constant relation to the actually realized egg production. This is shown by the figures presented in Table I. These give the counts of the number of oocytes on the ovary visible to the unaided eye in the case of a number of individuals. It will be understood that it is not contended that such counts give an accurate measure of the total oocyte content of the ovary. The figures, however, are so greatly in excess of what a hen actually ever lays that it may be quite safely concluded that in normal cases (where no accident or operation has induced regenerative processes in the ovary) all the eggs which will ever be laid (and usually more) are included among those visible to the eye, on an adult fowl's ovary.

From this table it is evident that when one bird has a winter record of twice what another bird has it is *not* because the first has twice as many oocytes in the ovary. On the contrary it appears that all birds have an anatomical endowment entirely sufficient for a very high degree of fecundity, and in point of fact quite equal to that possessed by birds which actually accomplish a high record of fecundity. Whether or not such high fecundity is actually realized evidently depends then upon the influence of additional factors beyond the anatomical basis.

4. This can only mean that observed differences (variations) in actual egg productions depend upon differences in the complex physiological mechanism concerned with the maturation of oocytes and ovulation.

TABLE I  
SHOWING THE NUMBER OF VISIBLE OÖCYTES IN THE OVARY OF CERTAIN BIRDS

Bird No.	Breed	Date of Hatching	Date Killed	Winter Egg Production	Ovarian Count			
					Discharged Follicles	Oocytes 1 cm. or Over in Diameter	Oocytes 1 mm. or Over in Diameter	Total Visible Oocytes
8,021	Barred Plymouth Rock...	June 1, '10	March 28, '11	3	17	9	53	1,149
8,017	Barred Plymouth Rock...	June 2, '10	March 30, '11	0	12	7	51	1,666
8,030	Barred Plymouth Rock...	June 1, '10	March 10, '11	0	8	5	62	839
8,005	Barred Plymouth Rock...	June 2, '10	March 14, '11	5	12	8	68	1,174
1,367	Barred Plymouth Rock...	April 28, '10	April 4, '11	3	49	7	29	2,306
8,018	Barred Plymouth Rock...	June 2, '10	March 24, '11	0	23	6	42	1,194
8,009	Barred Plymouth Rock...	June 2, '10	March 24, '11	0	17	6	49	2,101
8,010	Barred Plymouth Rock...	May 19, '10	March 17, '11	5	24	5	92	1,576
425	Barred Plymouth Rock...	March 30, '09	July 7, '10	0	21	12 <sup>3</sup>	142	1,521
2,546	White Leghorn <sup>4</sup> .....	May 18, '09	December 20, '10	54	75	5	231	2,452
2,067	White Leghorn.....	May 28, '09	December 15, '10	32	217	1	108	3,605
3,453	White Leghorn.....	May 21, '09	December 13, '10	0	11	5	75	1,701
3,833	White Leghorn.....	June 14, '09	December 22, '10	0	43	5	80	2,145
52	Cornish Indian Game....	April 21, '09	July 12, '10	13	54	6	167	1,550
71	F <sub>1</sub> Cross.....	March 31, '10	March 20, '11	106	50	5	70	2,000
.....	Guinea hen.....	?	January ... '11	...	9	3	36	765
.....	Guinea hen.....	?	January ... '11	...	3	3	38	545

<sup>3</sup> This includes 8 yolks in process of absorption.

<sup>4</sup> For this and the three following birds I am indebted to Professor James E. Rice, of Cornell University, who very kindly gave me these trap-nested individuals for use in the present study. The egg records in these cases are not the records for life, but the records up to November 1, 1910. The figures represent practically the total production.

<sup>5</sup> Birds not in laying condition when killed.

5. A study of winter egg production (taken for practical purposes as that from the beginning of the laying year in the early fall to March 1) proves that this is the best available measure of innate capacity in respect to fecundity, primarily because it represents the laying cycle in which the widest difference exists between birds of high fecundity and those of low fecundity.

6. It is found to be the case that birds fall into three well-defined classes in respect to winter egg production. These include (*a*) birds with high winter records, (*b*) birds with *low* winter records, and (*c*) birds which do not lay at all in the winter period (as defined above). The division point between *a* and *b* for the Barred Plymouth Rock stock used in these experiments falls at a production of about 30 eggs.

7. There is a definite segregation in the Mendelian sense of the female offspring in respect to these three fecundity divisions. This is demonstrated by extensive statistics in the complete report of this work. Here a single table only may be given by way of illustration, the one chosen being taken because all three classes are represented among the progeny of the particular type of mating with which it deals.

TABLE II

SHOWING THE RESULTS OF ALL MATINGS OF CLASS 4 B.P.R. ♂♂ × CLASS 1 B.P.R. ♀♀. GAMETIC CONSTITUTION:  $fL_1L_2 \cdot fl_1l_2 \times fL_1L_2 \cdot Fl_1l_2$

Number of Individuals Involved in Matings of this Type		Winter Egg Production of Daughters				
♂ ♂	♀ ♀	Class	Over 30	Under 30	Zero	Total Adult ♀ Progeny
4	17	Observed <i>Expected</i>	21 22.1	30 29.5	8 7.4	59
Mean winter egg production of all ♀ ♀ in indicated class . . . . .			48.85 eggs	16.34 eggs	0 eggs	

8. High fecundity may be inherited by daughters from their sire, independent of the dam. This is proved by the numerous cases presented in the detailed evidence where the same proportion of daughters of high fecundity are

produced by the same sire, whether he is mated with dams of low or of high fecundity.

9. High fecundity is not inherited by daughters from their dam. This is proved by a number of distinct and independent lines of evidence, of which the most important are: (a) continued selection of highly fecund dams does not alter in any way the mean egg production of the daughters;<sup>6</sup> (b) the proportion of highly fecund daughters is the same whether the dam is of high or of low fecundity, provided both are mated to the same male;<sup>7</sup> (c) the daughters of a fecund dam may show either high fecundity or low fecundity, depending upon their sire; (d) the proportion of daughters of *low* fecundity is the same whether the dam is of high or of low fecundity, provided both are mated to the same male.

10. A low degree of fecundity may be inherited by the daughters from either sire or dam or both.

11. The results respecting fecundity and its inheritance stated in paragraphs 3 to 10 inclusive are equally

<sup>6</sup> Pearl, R., "The Relation of the Results Obtained in Breeding Poultry for Increased Egg Production to the Problem of Selection," Rpt. 30th Meeting Soc. Proc. Agr. Sci., pp. (of reprint) 1-8, 1910; "Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen," Ann. Rpt. Amer. Breeders' Assoc., Vol. 6, pp. 317-326, 1911; "Inheritance of Fecundity in the Domestic Fowl," AMER. NAT., Vol. 45, pp. 321-345, 1911; "Breeding Poultry for Egg Production," Me. Agr. Expt. Sta. Ann. Rpt. for 1911, pp. 113-176. Pearl, R., and Surface, F. M., "Data on the Inheritance of Fecundity Obtained from the Records of Egg Production in the Daughters of '200-egg' Hens," Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 49-84 (Bulletin 166), 1909; "Studies on the Physiology of Reproduction in the Domestic Fowl. IV. Data on Certain Factors Influencing the Fertility and Hatching of Eggs," Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 105-164, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production," U. S. Dept. Agr., Bur. Animal Ind. Bulletin 110, Part I, pp. 1-80, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production," *Ibid.*, Part II, pp. 81-170, 1911.

<sup>7</sup> This is true, of course, only for certain gametic types of low fecundity females, as will be clear to any one who has studied the detailed evidence. This limitation, however, in nowise diminishes the force of this particular evidence in favor of the conclusion standing at the beginning of paragraph 9.

true for Barred Plymouth Rocks, Cornish Indian Games, and all cross-bred combinations of these breeds in  $F_1$  and  $F_2$ .<sup>8</sup>

The above statements are of definite facts, supported by a mass of evidence. Their truth is objective and depends in no way upon any theory of inheritance whatsoever. With this clearly in mind we may undertake their interpretation.

It is believed that these general facts, and the detailed results on which they are based, are completely accounted for and find their correct interpretation in a simple Mendelian hypothesis respecting the inheritance of fecundity in the fowl. This hypothesis involves the following points, each of which is supported by direct and pertinent evidence derived either from physiological and statistical studies of fecundity, or from the detailed data respecting the mode of inheritance of this character.

It is assumed in this hypothesis that:

1. There are three distinct and separately inherited factors upon which fecundity in the female fowl depends.

2. The first of these factors (which may be called the anatomical) determines the presence of an ovary, the primary organ of the female sex. The letter  $F$  is used throughout to denote the presence of this factor.

3. There are two physiological factors. The first of these (denoted by  $L_1$ ) is the basic physiological factor, which when present alone in a zygote with  $F$  brings about a low degree of fecundity (winter record under 30 eggs). This factor is under no limitations in gametogenesis, but may be carried in any gamete, regardless of what other factors may be also present.

4. The second physiological factor (denoted by  $L_2$ ) when present in a zygote together with  $F$  and  $L_1$ , leads to a *high* degree of fecundity (winter record over 30 eggs).

<sup>8</sup> And  $F_3$ . It was thought wise to delay publication any longer in order to include the data for  $F_3$ . It may be said, however, that they are in full accord with those which have been obtained from earlier cross-bred generations and the parent forms.



When  $L_1$  is absent, however, and  $L_2$  is present the zygote exhibits the same general degree of fecundity (under 30) which it would if  $L_1$  were present alone. These two independent factors  $L_1$  and  $L_2$  must be present together to cause high fecundity, either of them alone, whether present in one or two "doses," causing the same degree of low fecundity.

5. The second physiological factor  $L_2$  behaves as a sex-limited (sex-correlated or sex-linked) character, in gametogenesis, according to the following rule: The factor  $L_2$  is never borne in any gamete which also carries  $F$ . That is to say, all females which bear  $L_2$  are heterozygous with reference to it. Any female may be either homozygous or heterozygous with respect to  $L_1$ . Any male may be either homozygous or heterozygous with reference to either  $L_1$ ,  $L_2$  or both.

TABLE III

CONSTITUTION OF BARRED PLYMOUTH ROCK MALES IN RESPECT TO FECUNDITY

Class	Zygote	Gametes Produced
1	$fL_1L_2 \cdot fL_1L_2$	$fL_1L_2$
2	$fL_1L_2 \cdot fL_1l_2$	$fL_1L_2, fL_1l_2$
3	$fL_1L_2 \cdot fL_1l_2$	$fL_1L_2, fL_1l_2$
4	$fL_1L_2 \cdot fL_1l_2$	$fL_1L_2, fL_1l_2, fL_1l_2, fL_1l_2$
5	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2$
6	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2, fL_1l_2$
7	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2$
8	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2, fL_1l_2$
9	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2$

TABLE IV

CONSTITUTION OF BARRED PLYMOUTH ROCK FEMALES IN RESPECT TO FECUNDITY

Class	Zygote	$f$ -Bearing (♂ Producing) Gametes	$F$ -Bearing (♀ Producing) Gametes	Probable Winter Egg Production of ♀ of Indicated Zygotic Constitution
1	$fL_1L_2 \cdot FL_1l_2$	$fL_1L_2, fL_1L_2^9$	$FL_1l_2, FL_1l_2$	Over 30 eggs
2	$fL_1L_2 \cdot FL_1l_2$	$fL_1L_2$	$FL_1l_2$	Over 30 eggs
3	$fL_1l_2 \cdot FL_1l_2$	$fL_1l_2, fL_1l_2$	$FL_1l_2, FL_1l_2$	Under 30 eggs
4	$fL_1l_2 \cdot FL_1l_2$	$fL_1l_2$	$FL_1l_2$	Under 30 eggs
5	$fL_1l_2 \cdot FL_1l_2$	$fL_1l_2$	$FL_1l_2$	Zero eggs
6	$fL_1l_2 \cdot FL_1l_2$	$fL_1l_2$	$FL_1l_2$	Under 30 eggs

<sup>9</sup> The reason that gametes of the type  $fL_1l_2$  and  $FL_1l_2$  are not formed here will be evident on consideration. Since no gametes of type  $FL_2$  can, by

The different gametic constitutions in respect to fecundity which are to be expected in Barred Plymouth Rock males and females are shown in Tables III and IV.

Of these expected types six (1, 2, 3, 4, 7 and 8) were found and used in the experiments in the case of the males. In the case of the female class 5 birds were the only ones not actually tested out in the breeding experiments. Birds undoubtedly belonging to each of the omitted classes have been reared in the course of the experiments, but not yet submitted to continued breeding test.

The gametic constitutions of pure Cornish Indian Games in respect to fecundity are given in Tables V and VI.

TABLE V  
CONSTITUTION OF CORNISH INDIAN GAME MALES IN RESPECT TO FECUNDITY

Class	Zygote	Gametes Produced
1	$fL_1l_2 \cdot fL_1l_2$	$fL_1l_2$
2	$fL_1l_2 \cdot f l_1l_2$	$fL_1l_2, f l_1l_2$
3	$f l_1l_2 \cdot f l_1l_2$	$f l_1l_2$

TABLE VI  
CONSTITUTION OF CORNISH INDIAN GAME FEMALES IN RESPECT TO FECUNDITY

Class	Zygote	$f$ -bearing (♂ Producing) Gametes	$F$ -bearing (♀ Producing) Gametes	Probable Winter Egg Production of ♀ Indicated Zygotic Constitution
1	$fL_1l_2 \cdot FL_1l_2$	$fL_1l_2$	$FL_1l_2$	Under 30 eggs
2	$f l_1l_2 \cdot FL_1l_2$	$f l_1l_2, fL_1l_2$	$FL_1l_2, Fl_1l_2$	Under 30 eggs
3	$fL_1l_2 \cdot Fl_1l_2$	$fL_1l_2, f l_1l_2$	$Fl_1l_2, FL_1l_2$	Under 30 eggs
4	$f l_1l_2 \cdot Fl_1l_2$	$f l_1l_2$	$Fl_1l_2$	Zero eggs

It will be noted that C.I.G. ♀ classes 2 and 3 are gametically identical. Both are left in the table, however, since the whole table is so short that no confusion can be caused, and this example may make clear to some readers the nature of the compression (by omission of duplicate classes) which was practised in Tables III and IV.

How well this Mendelian hypothesis agrees with the facts has been shown in detail in the complete paper. By

hypothesis, be formed this implies that an interchange of the factors  $L_2$  and  $l_2$  between  $F$  and  $f$  gametes can not occur. The experimental proof of the truth of this conviction has been furnished in the case of the inheritance of the barred color pattern.

way of summary the following table shows the accord between observation and expectation for all matings of each general type taken together. For reasons set forth below, the lumped figures do not give an altogether fair estimate of the matter, but some sort of a summary is necessary.

TABLE VII

SHOWING THE OBSERVED AND EXPECTED DISTRIBUTIONS OF WINTER EGG PRODUCTION FOR ALL MATINGS TAKEN TOGETHER

Mating	Winter Production of Daughters			
	Class	Over 30	Under 30	Zero
All B.P.R. $\times$ B.P.R. ....	Observed	365½	259½	31
	Expected	381.45	257.25	17.30
All C.I.G. $\times$ C.I.G. ....	Observed	2	23	15
	Expected	0	25	15
All F <sub>1</sub> .....	Observed	36	79	8
	Expected	26.5	86.75	9.75
All F <sub>2</sub> and back-crosses <sup>10</sup> .....	Observed	57½	98½	23
	Expected	68.60	95.00	15.40

Considering the nature of the material and the character dealt with it can only be concluded that the agreement between observation and hypothesis is as close as could reasonably be expected. The chief point in regard to which there is a discrepancy is in the tendency, particularly noticeable in the B. P. R.  $\times$  B. P. R. and the F<sub>2</sub> matings, for the observations to be in defect in the "Over 30" class and in excess in the "Zero" class. The explanation of this is undoubtedly, as has been pointed out in the detailed paper, to be found in disturbing physiological factors. The high producing hen, somewhat like the race horse, is a rather finely strung, delicate mechanism, which can be easily upset, and prevented from giving full normal expression to its inherited capacity in respect to fecundity.

The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimentally studied warrants. It must be recognized as possible, if not indeed probable, that other

<sup>10</sup> With exception of one set of matings discussed in full in the complete paper.

racess or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. The directions in which deviations from the plan here found to obtain may, at least *a priori*, most probably be expected are two. These are: (a) differences in different breeds in respect to the absolute fecundity value of the factors which determine the expression of this character, and (b) gametic schemes which differ from those here found either in the direction of more or fewer distinct factors being concerned in the determination of fecundity, or in following a totally different type of germinal reactions.

Regarding the first point, it seems probable from the evidence in hand that the absolute fecundity value (*i. e.*, the degree of actual fecundity determined by the presence of the gametic factor) may differ for the factor  $L_1$  in the case of the Barred Rock as compared with the Cornish Indian Game breed. It is hoped later to take up a detailed study of this point, on the basis of the material here presented, and additional data now in process of collection. Whenever there is a difference in the absolute fecundity value of the  $L_1$  factor, it means that the division point for the classification of winter productions should be taken at a point to correspond with the physiological facts. Similarly, the absolute fecundity value of the excess production factor  $L_2$  may be different in different breeds. In applying the results of this paper to the production statistics of other breeds of poultry the possibility of differences of the kind here suggested must always be kept in mind.

The second point (the possibility of gametic schemes for fecundity differing qualitatively from that found in the present study) is one on which it is idle to speculate in advance of definite investigations. I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It can not justly be urged against the conclusions of this study that the Mendelian hypothesis advanced to account for the results is so complicated, and involves the assumption of so many factors or such complex interactions and limitations of factors, as to lose all significance. As a matter of fact the whole Mendelian interpretation here set forth is an extremely simple one, involving essentially but two factors. This surely does not indicate excessive complication. To speak in mathematical terms, by way of illustration merely, it may fairly be said that the formula here used to "fit" the data has essentially the character of a true graduation formula. The number of constants (here factors) in the formula is certainly much less than the number of ordinates to be graduated.

There is no assumption made in the present Mendelian interpretation which has not been fully demonstrated by experimental work to hold in other cases. That the expression of a character may be caused by the coincident presence of two (or more) separate factors, either of which alone is unable to bring it about, has been shown for both plants<sup>11</sup> and animals by a whole series of studies in this field of biology during the last decade. To find examples one has only to turn to the standard handbooks summarizing Mendelian work, as for example those of Bateson and Baur. Again sex-linkage or correlation of characters in inheritance has been conclusively demonstrated for several characters in fowls by the careful and thorough experiments of a number of independent investigators. Finally it is to be noted that Bateson and Punnett<sup>12</sup> have recently shown that the inheritance of the peculiar pigmentation characteristic of the silky fowl follows a scheme which in its essentials is very similar to that here worked out for fecundity.

<sup>11</sup> Particularly important here are the brilliant researches of Nilsson-Ehle on cereals, and of Baur on *Antirrhinum*.

<sup>12</sup> Bateson, W., and Punnett, R. C., "The Inheritance of the Peculiar Pigmentation of the Silky Fowl," *Journal of Genetics*, Vol. 1, pp. 185-203.

## THE SELECTION PROBLEM

The results of the present investigation have an interesting and significant bearing on the earlier selection experiments on fecundity at this station. It is now quite plain that continued selection of highly fecund females alone could not even be expected to produce a definite and steady increase in average flock production. The gametic constitution of the male (in respect especially to the  $L_2$  factor) plays so important a part in determining the fecundity of the daughters that any scheme of selection which left this out of account was really not "systematic" at all, but rather almost altogether haphazard. It is repeatedly shown in the detailed account of these experiments that the same proportion of daughters of high fecundity may be obtained from certain mothers of low fecundity as can be obtained from those of high fecundity provided that both sets of mothers are mated to males of the same gametic constitution. What gain is to be expected to accrue from selecting high laying mothers under such circumstances, at least so far as concerns the daughters?

"Selection" to the breeder means really a system of breeding. "Like produces like," and "breed the best to get the best"; these epitomize the selection doctrine of breeding. It is the simplest system conceivable. But its success as a system depends upon the existence of an equal simplicity of the phenomena of inheritance. If the mating of two animals somatically a little larger than the average always got offspring somatically a little larger than the average, breeding would certainly offer the royal road to riches. But if, as a matter of fact, as in the present case, a character is not inherited in accordance with this beautiful and childishly simple scheme, but instead is inherited in accordance with an absolutely different plan, which is of such a nature that the application of the simple selection system of breeding could not possibly have any direct effect, it would seem idle to

continue to insist that the prolonged application of that system is bound to result in improvement.

It seems to me that it must be recognized frankly that whether or not continued selection of somatic variations can be expected to produce an effect on the race depends entirely on the mode of inheritance of the character selected. In other words, any systematic plan for the improvement of a race by breeding must be based and operated on a knowledge of the gametic condition and behavior of the character in which improvement is sought, rather than the somatic. Continued mass selection of somatic variations as a system of breeding, in contrast to an intelligent plan based on a knowledge of the gametic basis of a character and how it is inherited, seems to me to be very much in the same case as a man who, finding himself imprisoned in a dungeon with a securely locked and very heavy and strong door with the key on the inside, proceeded to attempt to get out by beating and kicking against the door in blind fury, rather than to take the trouble to find the location of the key and unlock the door. There is just a possibility that he could finally get out in a very few instances by the first method, but even in those cases he would be regarded by sensible men as rather a fool for his pains.

Of course what has been said is not meant to imply that selection, on the basis of somatic conditions may not have a part in a well considered system of breeding for a particular end. In many cases it certainly will have. Thus in the case of fecundity in the fowls, selection of mothers on the basis of fecundity records is essential in getting male birds homozygous with respect to  $L_1$  and  $L_2$ . But the point which seems particularly clear in the light of the present results is that blind mass selection, on the basis of somatic characters only, is essentially a haphazard system of breeding which may or may not be successful in changing the type in a particular case. There is nothing in the method *per se* which insures such success, though that there is inherent potency in the

method *per se* is precisely the burden of a very great proportion of the teaching of breeding (in whatever form that teaching is done) at the present time.

It seems to me that it has never been demonstrated, up to the present time, that continued selection can do anything more than:

1. Isolate pure biotypes from a mixed population, which contains individuals of different heredity constitution in respect to the character or characters considered.

2. Bring about and perpetuate as a part of a logical system of breeding for a particular end, certain combinations of hereditary factors which would never (or very rarely) have occurred and would have been lost in the absence of such systematic selection; which combinations give rise to somatic types which may be quite different from the original types. In this way a real evolutionary change (*i. e.*, the formation of a race of qualitatively different hereditary constitution from anything existing before) may be brought about. This can unquestionably be done for fecundity in the domestic fowl. But here "selection" is simply one part of a system of breeding, which to be successful must be based on a definite knowledge of gametic as well as somatic conditions. It is very far removed from a blind "breeding of the best to the best to get the best." The latter plan alone may, as in the case of fecundity, fail absolutely to bring about any progressive change whatever.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued. To determine, by critical experiments which shall exclude beyond doubt or question such effects of selection as those noted under 1 and 2 above, whether the absolute somatic value of factors may be changed by selection, or in any other way, is one of the fundamental problems of genetics.